The well-behaved killer: Late Pleistocene humans in Eurasia were significantly associated with living megafauna only

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ABSTRACT

The end of the Pleistocene was characterized by an intense, highly selective extinction event, affecting large-bodied terrestrial mammals worldwide. This period coincides with two major events, the last glacial period, and the dispersal of technologically advanced *Homo sapiens* outside the Old World. Upper Paleolithic hunters were armed with advanced, projectile weapons, and were able to dispatch prey as large as mammoths. As human population size was rapidly expanding, and hence means meat consumption rate was also growing, Paleolithic hunters are often held responsible for the extinction of mammalian megafauna. Yet, whether human focused on megafauna as prey, and drove them to extinction, remains uncertain. Here we model spatial and temporal patterns in habitat suitability for 24 megafauna species and *Homo sapiens* in Eurasia. We find that within land patches most suitable for humans, the identity of the most abundant herbivorous mammals switched from warm adapted species (such as the wild boar) to cold adapted species (reindeer) as climate switched from mild to cold conditions. Importantly, extinct herbivorous megafauna species were consistently rare within habitat patches optimal for humans. This suggests that humans may have settled under relatively constant climatic conditions, and possibly behaved as efficient predators, exploiting their prey in a cost-effective manner. These results are in accordance with evidence coming from the archaeological record, where medium sized living herbivore species are overrepresented in comparison of their natural abundance. For Late Pleistocene megafauna in Eurasia, human hunting may have been just an additional, non-decisive extinction factor.

1. Introduction

The increased technological competence and abundance of late Paleolithic and Neolithic hunters was contemporary to the massive wave of extinction that affected the megafauna (i.e., large mammals) at the end of the Pleistocene. As many as 177 mammal species above 10 kg in body size disappeared from all continents between the last interglacial (120 ka) and the start of the Holocene (Sandom et al., 2014). Human hunting is often portrayed as the main driver of megafauna decline, an idea dubbed the 'overkill hypothesis' (Martin, 1966; Mosimann and Martin, 1975; Alroy, 2001). However, it is unknown whether human hunting could have been sufficiently intense to drive megafauna species to extinction (Grayson and Meltzer, 2003; Lima-Ribeiro and Diniz-Filho, 2013), especially in the Old World, where the intensity of species loss was comparatively lower than elsewhere (Faith, 2014; Sandom et al., 2014). Overkill models usually do not take into consideration that in modern hunter-gatherer societies, big-game hunting may be disconnected from calorie procurement per se, and linked to prosocial functions, such as gaining better mating opportunities (Hill and Hurtado, 2009; Hill et al., 2013). Field surveys indicate food gathering and fishing may provide as many calories and proteins as big-game hunting in such societies (Ember, 1978), and that hunter-gatherers make extensive use of food resources other than vertebrate meat (Stiner, 2013; Morgan, 2015; Zaatari et al., 2016; Sullivan et al., 2017). To understand whether humans may have driven megafauna to extinction, it is necessary to consider simultaneously the climatic preferences of both potential prey species and humans. This is because species with similar climatic requirements tend to coexist, and a correct

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evaluation of the potential impact of hunting on prey populations depends on prey availability to the hunters (Lorenzen et al., 2011). Modern methodologies and data now allow profiling climatic preferences for fossil species. Past climates, modeled by extending simulations of atmospheric and oceanic circulation models (AOGCM) back in time at fossil occurrences, are useful to 'learn' the climatic preferences of fossil species (Svenning et al., 2011). Such techniques, known as species distribution models (SDMs), thereby provide detailed maps of species occurrence probability in the past (e.g., Di Febbraro et al., 2017). Recent studies demonstrate a positive and significant relationship between such occurrence probability maps and real local abundance, in both vertebrates (VanDerWal et al., 2009; Weber et al., 2016) and plants (e.g. Fois et al., 2018). Thus, SDMs have the potential to tell where and when a given species might be expected to have been abundant.

We collected occurrence data for Late Pleistocene mammal species and *Homo sapiens* in Eurasia, and intersected occurrences with paleoclimatic data. Then, we built SDMs for these species to derive their habitat suitability maps. This allows us to ascertain which potential prey species were abundant where humans occurred the most. Under the overkill scenario, the distribution of optimal (i.e., most suitable) habitat patches for humans must overlap with that of the extinct megafauna. In contrast, humans might have been alternatively associated with different prey species in keeping with changing climatic regimes, which would suggest they had the potential to exploit different game species at different times. We drew megafauna and *H. sapiens* occurrence probability maps over the last 40 ka in Eurasia by using SDMs. After partitioning species into groups according to their body size, feeding category, and status (i.e., whether they were large or medium-sized, carnivorous or herbivorous, and extinct or extant), we compared ecological groups for their degree of geographical overlap to the range of *H. sapiens*. Then, we contrasted species habitat suitability values within the core of *H. sapiens* presumed distribution, where human occurrence was probably the highest.

2. Material and methods

2.1. Climatic predictors

Paleoclimatic variables were derived from AOGCM simulations of past climates (Singarayer and Valdes, 2010), provided from 72 to 8 ka with a temporal resolution of 4 kyr, and downscaled at 0.5° of spatial resolution (Maiorano et al., 2013). Specifically, the data include four climatic predictors: i) mean temperature during summer (warmest quarter), ii) mean temperature during winter (coldest quarter), iii) mean precipitation during summer (mean precipitation during the warmest quarter) and iv) mean precipitation during winter (mean precipitation during the coldest quarter). We re-projected them into a Mollweide equal area coordinate reference system at a final spatial resolution of ~50 km. We tested for the absence of multicollinearity among the four predictors, reporting a variance inflation factor < 5 (Zuur et al., 2010).

2.2. Homo sapiens record

We removed from the Canadian Archaeological Radiocarbon Database (CARD; Gajewski et al., 2011) occurrences with uncertain archaeological attribution, or where the identity of the *Homo* species (either *H. neanderthalensis* or *H. sapiens*) was uncertain. Then, we pruned the data from radiocarbon dates not obtained by using Accelerator Mass Spectrometry (AMS), and limited the age range in between 40 and 10 ka. Although climatic data extend before 40 ka, *H. sapiens* presence in Eurasia before this age is limited geographically to the Middle East. Still, radiocarbon dates before 40 ka are very unstable, and the extinction wave of large mammals in the Old World started some 40 ka (Sandom et al., 2014). AMS dates were calibrated with the

IntCal13 curve, by using the R package Bchron (Parnell, 2016). Ages are presented as calibrated dates (calBP). Our database includes 2429 *H. sapiens* fossil occurrences. To compute SDMs, we removed duplicated records occurring in the same cell of the climatic grid used for model calibration (see below). The database of *H. sapiens* record used in this study is provided in Table S1.

2.3. Mammal fauna record

To construct this database, we started from the late Pleistocene fossil large mammal database published in Carotenuto et al. (2016). Whereas, for humans, we considered a temporal interval between 40 and 10 ka, for the megafauna, we extended the data back to 72 ka, which is the limit of the palaeoclimatic data. Faunal remains are less intensely studied, and archaeological sites can be readily identified by stone implements, which have much better preservation potential than bone. Therefore, the mammal record is less dense than the archaeological record. By extending the faunal database back in time, we could have comparable number of occurrences for both humans and the other large mammal species, which is a necessary prerequisite for proper SDM calibration (see below). Our faunal database includes 4965 Eutherian mammals occurrences distributed over 749 fossil localities for 24 either extinct or extant species belonging to the orders of Artiodactyla, Carnivora, Perissodactyla and Proboscidea. The extinct species group includes ten species: *Coelodonta antiquitatis*, *Crocuta crocuta*, *Bison priscus*, *Bos primigenius*, *Elephas antiquus*, *Mammuthus primigenius*, *Megaloceros giganteus*, *Stephanithinus hemitoechus*, *Equus hydruntinus*, *Ursus spelaeus*. Fourteen species analyzed are still living today: *Alces alces*, *Canis lupus*, *Capra ibex*, *Capreolus capreolus*, *Cervus elaphus*, *E. ferus*, *Lynx lynx*, *Panthera leo*, *Rangifer tarandus*, *Rupicapra rupicapra*, *Saiga tatarica*, *Sus scrofa*, *U. arctos*, *Vulpes vulpes*. The record was prepared by collating information of georeferenced fossil localities, including estimated ages and faunal lists, coming from the following databases: the Fossilworks database (http://fossilworks.org/?a = home), the NOW database (http://www.helsinki.fi/science/now/) and data provided in Raia et al. (2009) and Carotenuto et al. (2010, 2015). We fully revised synonyms and assigned the species names to the most recent accepted scientific name and excluded remains with uncertain identification at the species level. We reported biochronological or radiometric estimates for ages of individual fossil localities. For localities with non-radiometric dating, we assigned a numerical age estimate by using spectral ordering. This method works by ordering fossil localities according to their taxonomic similarity. The matrix of locality similarity is decomposed and the Fiedler eigenvector (the second smallest eigenvalue of the Laplacian matrix) extracted. Such vectors provide the ordination of localities according to their temporal sequence (Fortelius et al., 2009). The decomposition further assigns a Fiedler score to each locality. The scores are regressed against known radiometric age estimates, and the regression coefficients used to infer ages for all of the localities with no available age estimate (see Raia et al., 2009 and Carotenuto et al., 2010 for full details).

For SDM calibration, after the numerical dating procedure, we applied to the mammal species record the same set of filtering criteria as with the *H. sapiens* record (i.e., removing duplicate records per cell), to end up with an average sample size of 150 occurrences (min = 21, max = 325) per species.

The faunal record was finally supplemented with species body size data as published in Raia et al. (2011, 2013) and Carotenuto et al. (2010). The faunal database is provided in Table S1.

2.4. Species distribution models

To produce SDMs, we first divided the fossil record of both humans and large mammals into successive 4 ka long time bins. Subsequently, we randomly generated 10,000 background points over Eurasia, which were used for SDMs calibration. The 10,000 background points were

partitioned across time bins, in proportion to the number of fossil localities falling into a particular bin. For each bin, we extracted climate data at each occurrence and background point. As the ensemble of climatic data over species existence (i.e., across temporal bins) provides the closest approximation of the species fundamental niche (Nogués-Bravo, 2009; Maiorano et al., 2013), we calibrated a single SDM for each species by pooling occurrence data across temporal bins. We trained SDMs by using an ensemble forecasting approach, as implemented in the *biomod2* package (Thuiller et al., 2009) within the R environment (R Core Team, 2016). To produce SDMs we applied four different algorithms: Generalized Linear Models (GLMs); Generalized Additive Models (GAMs), Generalized Boosted Regression Models (GBMs) and Maximum Entropy (MAXENT). We randomly split each species occurrence dataset into a 70% sample, used for the calibration of the model, and the remaining 30%, used to evaluate models predictive performance. The latter was assessed by two different metrics, the area under the receiver operating characteristic curve (AUC; Swets, 1988) and the Boyce index (Hirzel et al., 2006). We repeated such splitting procedure 10 times, and then averaged evaluation scores and model projections. To avoid using poorly calibrated models, only the projections from the models with AUC > 0.75 were considered in the subsequent analyses. Models were averaged calculating a weighted mean by model's AUC (Marmion et al., 2009). In details, for Eurasian large mammals SDMs were trained in the time frame from 72 to 8 ka, whereas for *H. sapiens* models were trained from 40 to 8 ka. For all the species models were projected over Eurasia on each time interval spanning from 40 to 10 ka (that is within the human record range). Continuous models projections were transformed into binary, presence/absence maps, using the threshold that maximizes the sum of sensitivity and specificity (Maiorano et al., 2013; Di Febbraro et al., 2015; Liu et al., 2016, 2018). To assess the effect of model extrapolation on the values of predictor variables lying outside the training range, i.e., projecting models on non-analogous climates (Nogués-Bravo, 2009), we calculated the Multivariate Environmental Similarity Surface (MESS) index (see Table S2), following Elith et al. (2006)

2.5. Spatial association between mammal fauna and Homo sapiens

To assess how *H. sapiens* spatially associated to other predators and potential prey (i.e., large herbivores), we divided the large mammal species according to their status (extant or extinct), their body mass (large or medium-sized) and their presumed diet (herbivores or carnivores). As regards body mass, we split primary consumers into a large- and a medium-sized category, depending on whether their estimated body size was either more or < 1000 kg (megaherbivores and meso-herbivores in the classical sense, Owen-Smith, 1988; Mondanaro et al., 2017). Among carnivores, we considered to be 'large' those species with estimated body size > 45 kg, and 'medium-sized' species < 45 kg in body size (Bekoff et al., 1984). These criteria originate eight ecological categories: 'Extinct Large Herbivores', 'Extinct Medium Herbivores', 'Extinct Large Carnivores', 'Extinct Medium Carnivores', 'Extant Large Herbivores', 'Extant Medium Herbivores', 'Extant Large carnivores' and 'Extant Medium Carnivores'. We used the group affiliation as the response variable in a multinomial logistic regression model. As explanatory variables, we produced the following five covariates derived from the SDMs output:

1) Predictor 1 (CLIMATIC PLASTICITY) represents the degree of climatic conservatism, which is the tendency to seek after constant environmental conditions under climatic change. Predictor 1 is based on MESS values derived by SDMs (Fig. 1B). MESS is calculated as the environmental similarity between a given site (e.g. predictors raster cells) with a reference list of points (usually species occurrences), according to a given set of environmental variables. A Ratio MESS between successive time intervals is computed as:

Ratio MESS = MESS species/MESS total

where MESS species refers to MESS values obtained comparing each cell of predicted presence in time interval j with cells of predicted presence in time interval j + 1. MESS total indicates MESS values calculated over all the cells, irrespective of where the species is predicted to occur (with this being a metric for the intensity of climatic change between successive intervals). High values of Ratio MESS indicate that a species occupied similar climates under constant climatic conditions or, alternatively, that the species sought after constant environmental conditions under dramatic climatic change (i.e. high climatic plasticity in our sense). Whatever the case, the higher Ratio MESS, the more constant climatic preferences for the species were.

2) Total area of the species most suitable territories ("PIXEL95", Fig. 1C, the total geographic area where the habitat was highly-suitable to the focal species). PIXEL95 counts the number of pixels above the 95th percentile of the suitability distribution for the focal species. Therefore, it represents the total area where the species is presumed to be abundant.
3) This predictor ("PIXEL95H") is the mean suitability value of the focal species within *H. sapiens* PIXEL95 (Fig. 1D).
4) Degree of overlap (OVERLAP, Fig. 1E) between the focal species and *H. sapiens* in terms of area of predicted geographical ranges. This was calculated as the ratio between the count of pixels shared by both the focal species and *H. sapiens*, and the total count of pixels obtained by combining the maps of the two.
5) Range shift over time (DISTANCE, Fig. 1F) is the extent of range shift over successive time intervals. DISTANCE is calculated as the Euclidean distance between the centroids of species predicted ranges over consecutive time bins. Centroids were located by weighing the suitability values predicted within the species range per bin. In theory, high values of both predictors 1 and 5 indicate habitat tracking.

We performed a multinomial logistic regressions between species ecological categories and predictors, setting a single category as the reference. This helps telling the ecological differences between categories in reference to human presence and climatic variability. The regressions were computed over consecutive time bins, but they were repeated adopting a temporal moving window approach to account for fossil localities age uncertainty. For the temporal window approach, we took predictors averages computed over three consecutive, overlapping temporal intervals. For instance, for five consecutive bins 1, 2, 3, 4, and 5, the first group of bins spans from 1 to 3, the second from 2 to 4, the third from 3 to 5 and so on. This way, we get new predictor maps each one averaged over three original consecutive ones, except for the penultimate interval, whose moving window spans over two intervals only (i.e. intervals 4 and 5 in the fictionary example above). Under each approach, we calculated multinomial logistic regressions on the entire species pool, and then by testing herbivorous and carnivorous taxa separately.

To further investigate spatial association between mammal fauna and *H. sapiens,* we calculated statistical relationships between *H. sapiens* suitability values inside its PIXEL95 map and the corresponding suitability values of each mammal species inside PIXEL95H, averaging suitabilities over all time bins. We performed linear regressions both univariate (i.e., species by species) and multivariate (all herbivorous species together), as to explore whether *H. sapiens* was associated to different species under different climatic conditions. We ranked species by partial regression coefficients, and applied Wilcoxon Signed-Rank test comparing pairs of consecutive bins for the identity (and rank) of the herbivore species most associated to *H. sapiens*. This analysis tells whether the rank-abundance (actually rank-suitability) distribution of large herbivores within the human range did change from one period to the next.
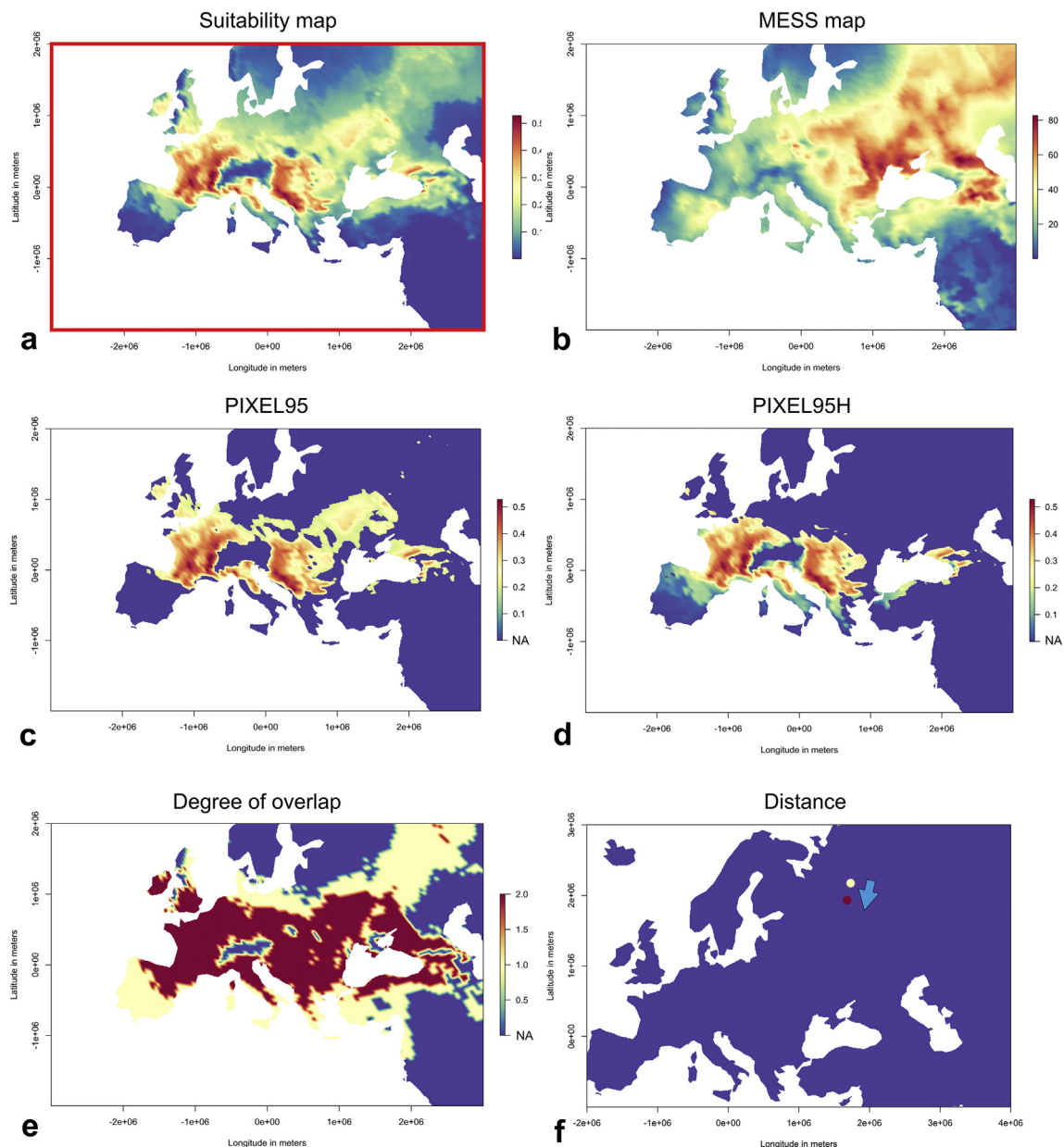
Fig. 1. Species Distribution Models output (A) and the derived variables (B, C, D, E, F) used in the analyses. We present data for the wholly mammoth during the Last Glacial Maximum (~24 ka) as an example. A) Suitability map of the species. Colour gradient indicates increasing values of suitability from the lowest (violet) to the highest (red). All the other variables were derived from this map. B) Raw MESS map used to compute the CLIMATIC PLASTICITY of the species. C) PIXEL95 is the map showing suitability values higher than the 95th percentile for the considered species. D) PIXEL95H is the map of species suitability values included in the space delimited by the *Homo sapiens* PIXEL95. E) Map showing the degree of overlap between the predicted distribution of *H. sapiens* and the wolly mammoth. Red pixels indicate the geographical overlap, yellow values indicate not-overlapping regions and violet pixels indicate no predicted geographic distributions. F) Map showing wolly mammoth's distribution centres in two consecutive time intervals. The yellow point indicates the distribution centre during ~28 ka and the red one indicates the distribution at ~24 ka. The arrow indicates the computed Euclidean distance between the two centres. This figure represents a truncated portion of the whole study area, Eurasia, corresponding to *H. sapiens* territories with high suitability values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We finally assessed the differences in mean and variance of climate conservatism between *H. sapiens* and its most positively associated species as emerged from the regression models illustrated above. Before testing for differences, climate conservatism values were standardized separately for each time bin by dividing each species climate conservatism by the highest value for the given time bin. Climate conservatism differences in mean were tested using Wilcoxon Signed-Rank test, while differences in variance were evaluated using modified Brown-Forsythe Levene-type test (Fox, 2002).

3. Results

3.1. SDM evaluation

SDMs reached excellent predictive performances for most of the species (sensu Swets, 1988), reporting AUC values between 0.884 and 0.980, with a median value of 0.944 and only three species scoring AUCs < 0.9. Boyce index values ranged in between 0.136 and 0.981, with a median value of 0.793. Only three species reported Boyce < 0.5. According to the MESS analysis results, negligible or no
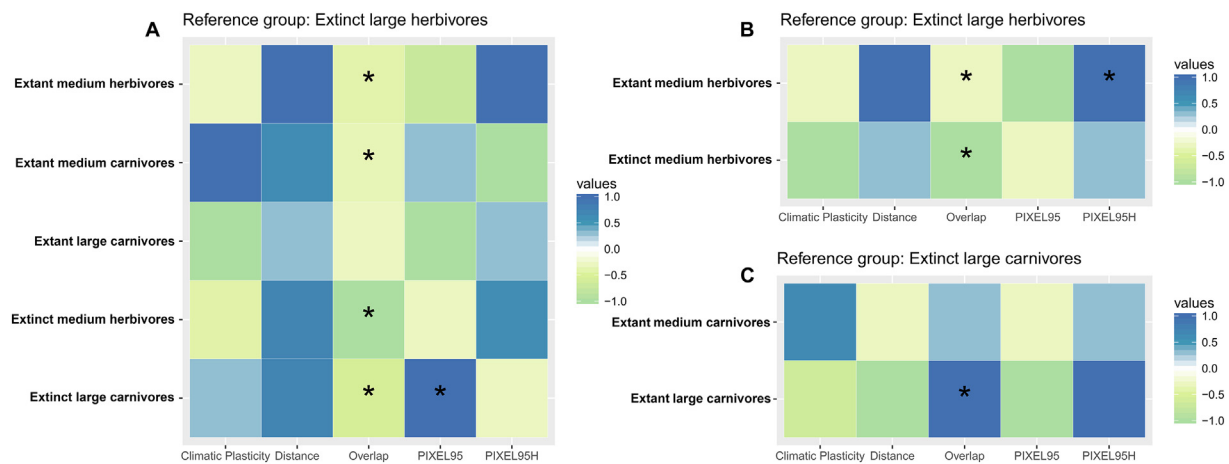
Fig. 2. The relationship between humans and different ecological groups of the a) entire megafauna, b) herbivores and c) carnivores analyzed separately. In blue tones, the focal ecological group has higher values than the reference group, the opposite applies to green tones. Climatic Plasticity = the similarity in climatic conditions experienced by individual species across temporal intervals. Distance = the distance between the centroid of the species distributions across intervals. Overlap = degree of overlap between each group and the human range. PIXEL95 = extent of areas of high suitability per group. PIXEL95H = extent of areas of high suitability per group within the core of geographic range of *H. sapiens*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

extrapolation effect emerged in SDMs predictions for each species and time interval (Table S2).

3.2. Multinomial logistic regressions

When including all the species in the multinomial logistic regressions, extinct large carnivores (slope = −1.412; *p* value = 0.003), extant medium carnivores (slope = −0.672, *p* value = 0.026), extinct medium herbivores (slope = −3.060, *p* value = 0.002) and extant medium-sized herbivores (slope = −0.856, *p* value < 0.001) showed a significantly lower overlap with *H. sapiens* geographic range than the reference (i.e., extinct large herbivores). In addition, extinct large carnivores showed significantly higher values of abundance in PIXEL95 map than the reference (slope = 1.014, *p* value = 0.049; the AIC of the complete model is 541.952, see Fig. 2 and Supplementary Table S3.1 for detailed results).

When considering herbivore species only, both extinct and extant medium herbivores showed a significantly lower overlap with *H. sapiens* geographic range than the reference group (extinct large herbivores; slope = −2.470, *p* value = 0.010; slope = −0.737, *p* value = 0.001, respectively). Besides, extant medium herbivores reported a significantly higher abundance than reference group within the most suitable portion of *H. sapiens* geographic extent (i.e., PIXEL95H; slope = 2.650, *p* value = 0.041; Fig. 2; the AIC of the complete model is 219.660).

According to multinomial regressions on carnivore species only, large-sized extant carnivores exhibited a significantly higher overlap with *H. sapiens* range than the reference group (extinct large carnivores; slope = 2.226, *p* value = 0.022; Fig. 2; the AIC of the complete model is 114.461). The complete list of all the regression results (including the temporal window approach) is available in the Table S3.

3.3. Species-wise regression models on suitability values

Overall, we found positive and significant relationships between the averaged suitability values of focal species and those of *H. sapiens*. For ease of interpretation, we divided our results according to the sign and magnitude of the regressions slopes (Fig. 3). Specifically, we found positive and significant relationships between *H. sapiens* and the following species (ordered with decreasing slope values): *V. vulpes, E. ferus, C. crocuta, C. elaphus, B. primigenius, R. rupicapra, S. scrofa, U. spelaeus, S. hemitoechus, C. capreolus, C. ibex, E. hydruntinus, E. antiquus,*

R. tarandus, C. lupus and *P. leo* (see Table S4). *L. lynx, A. alces, M. giganteus, B. priscus* showed a negative and significant relationship (see Table S4).

3.4. Multiple regression models on suitability values

We found significant and positive relationships between several species and *H. sapiens* suitability values (Fig. 4; all the regressions results can be found in the Table S5). For the time bin 40–36 ka, we found significant and positive relationships for *E. ferus, S. scrofa, U. spelaeus* and *B. primigenius*. Positive and significant results for *S. scrofa, E. ferus* and *C. crocuta* emerged for the interval 36–32 ka. For the temporal bin 32–28 ka, we found the following species positively associated to *H. sapiens*: *E. ferus, B. primigenius* and *U. spelaeus*. During the interval 28–24 ka, *S. scrofa, C. crocuta, R. tarandus* and *U. spelaeus* were positively related to *H. sapiens*. During the time bin 24–20 ka, we found *C. crocuta, R. tarandus, E. ferus* and *U. spelaeus* to be positively related to humans. For the interval 20–16 ka, regression models show a positive relationship between *S. scrofa, C. crocuta, V. vulpes* and *B. primigenius* to be positively related to *H. sapiens* suitability values. For the interval 16–12 ka, we found *C. elaphus, E. ferus, B. primigenius, U. spelaeus* and *M. primigenius* to be positively related to humans. During the last interval (12–8 ka), we found positive and significant relationships between *H. sapiens* and *C. elaphus, M. primigenius, P. leo* and *V. vulpes* (see Table S5.1 and S5.2 for detailed results and negative associations).

Wilcoxon signed rank test indicated a significant change in the faunal composition related to *H. sapiens* PIXEL95 for the temporal intervals 32–24, 24–16 and 20–12 ka (w = 50, *p* = 0.016; w = 75, *p* = 0.047; w = 70, *p* = 0.029, respectively; see Table S6 for detailed results).

3.5. Differences in climatic conservatism between Homo sapiens and other large mammals

We calculated differences in mean and variance of climatic conservatism between *H. sapiens* and the species group including *E. ferus, C. elaphus, B. primigenius, R. rupicapra* and *S. scrofa* as these taxa showed a significant, positive association with *H. sapiens* (see above). In particular, *H. sapiens* showed a significantly higher mean climate conservatism along the time bins (w = 267, *p* = 0.003; Fig. 5) than the selected fauna, also showing a significantly lower variance (L = 1.74, *p* = 0.048).
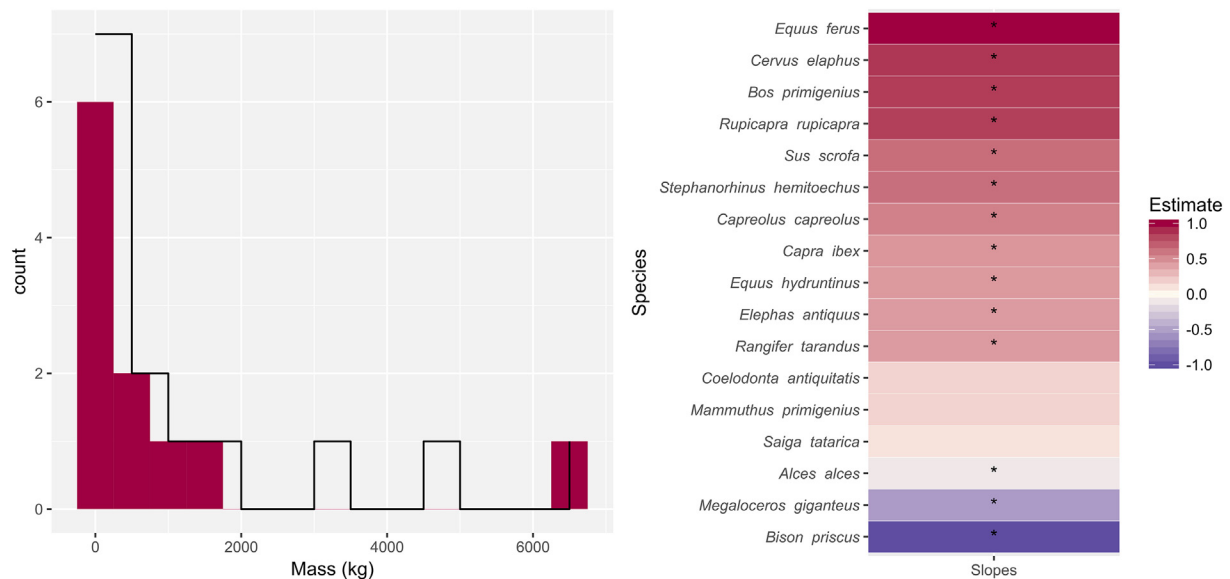
Fig. 3. Left: body size distribution of herbivore megafauna species associated with humans (red bars) and total body size distribution (open bars). Right: results of the regression of suitability of individual species versus human suitability. Significant regression slopes are indicated with the asterisk. Positive relationships are represented by red tones, negative relationships by blue tones. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Extinct large herbivores presented the highest geographic range overlap with *H. sapiens* (Fig. 2a,b). This indicates humans theoretically had very good chance of encountering the extinct megafauna, in keeping with the overkill scenario. However, extant medium-sized herbivores showed significantly higher values of suitability than extinct large herbivores within the core of human distribution (i.e., PIXEL95H, Fig. 2b). Taken together, the results indicate humans were more abundant in habitat patches where populations of extant medium-sized herbivores were abundant. In keeping with our findings, the

archaeological record indicates that species of deer, the auroch, and the wild boar were humans' preferred preys (Stewart, 2004; Stiner and Kuhn, 2006; Stiner et al., 2008). Although the exploitation of proboscidean carcasses seems to be a typical behavior of Paleolithic humans (Shipman, 2015), evidence for direct killing of mammoths and elephants is rare (Gaudzinski et al., 2005). The record also tells human hunters started focusing their foraging activities on the reproductive core (prime adults) of small game species (such as deer and bovids) at least since 100 ka (Stiner and Kuhn, 2006; Stiner, 2013). Hunting prime adults could be potentially dangerous to the prey populations as it can unsettle their long-term survival. Yet, by switching between alternative
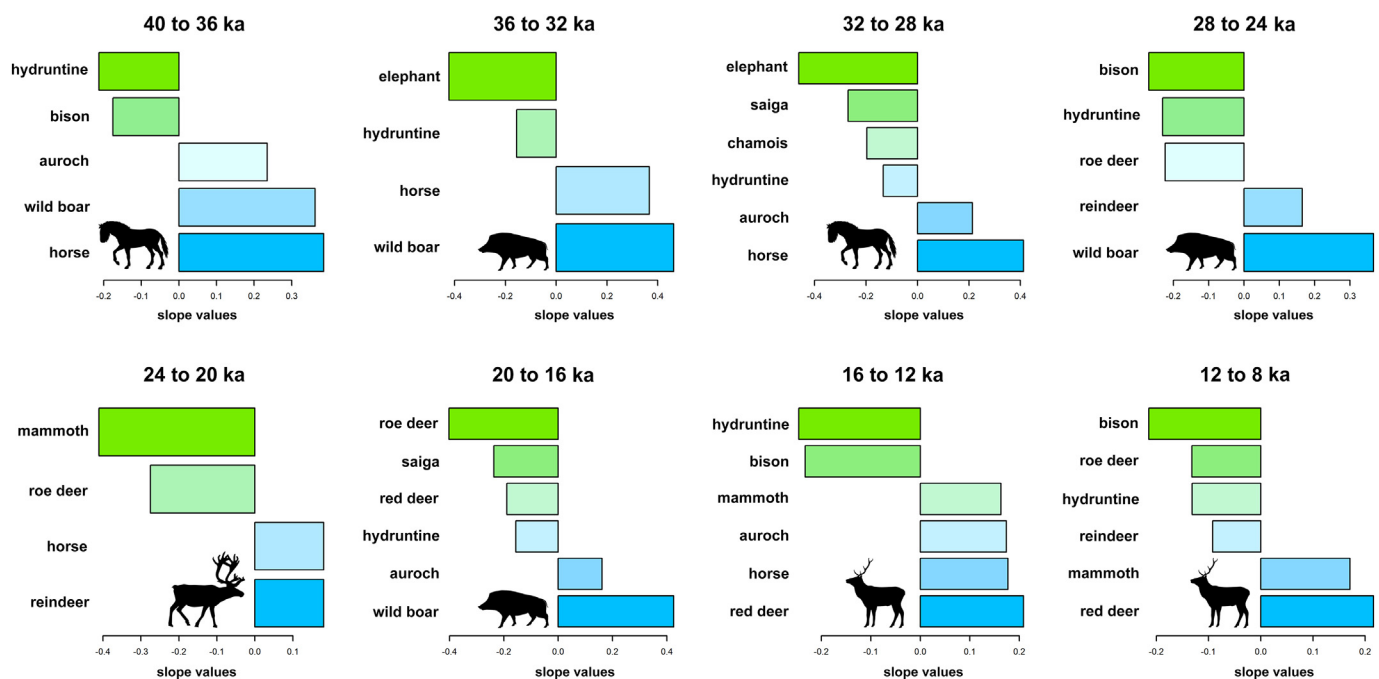

Fig. 4. Plot of the species statistically associated to humans per time period, partitioned into 4 kyr long intervals. The bars in blue tone represent species positively associated to humans, bars in green tones represent species negatively associated to humans. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
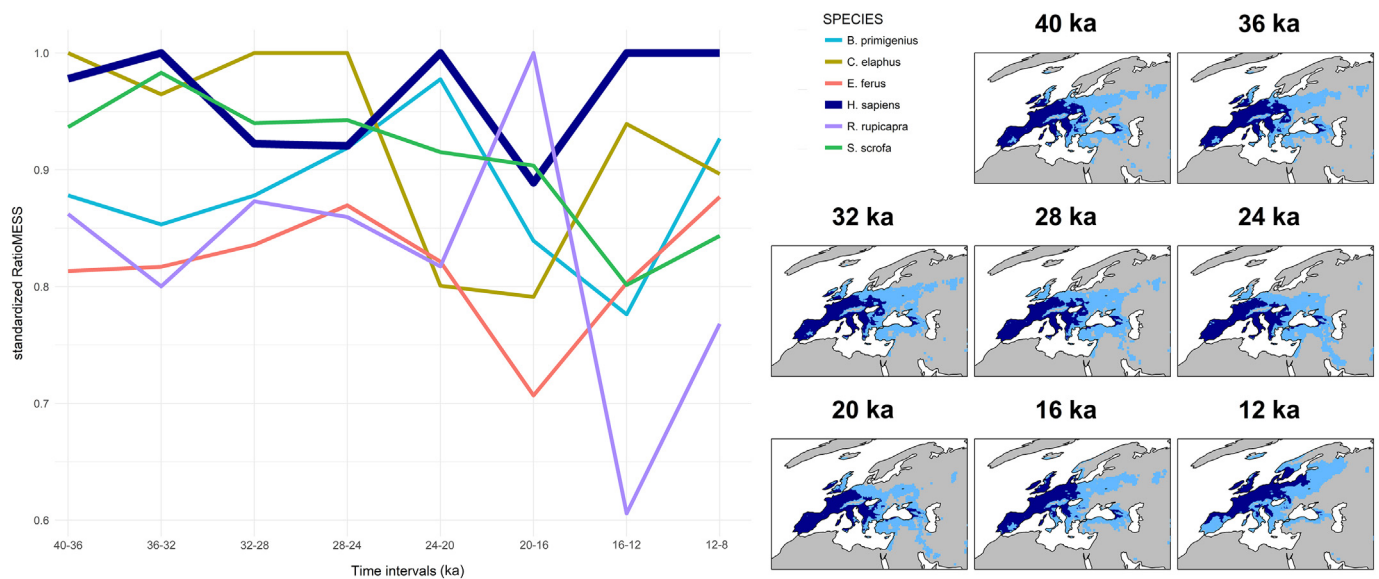
Fig. 5. Climatic plasticity across temporal intervals in *H. sapiens* and the species most closely associate to it (left), and evolution of *H. sapiens* suitability maps (right). Dark blue indicates the core of *H. sapiens* distribution (i.e., above the 95th percentile of suitability values), while light blue refers to the entire *H. sapiens* distribution. This figure represents a truncated portion of the whole study area, Eurasia, corresponding to *H. sapiens* territories with high suitability values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

prey and food sources (Zaatari et al., 2016) according to their availability (Fig. 4), and expanding their dietary niche as to include seafood, small mammals, tortoises, and birds (Stiner, 2013; Zaatari et al., 2016), humans may have favoured long-term survival of their preferred prey. The focus on prime adults (which are the most difficult individuals to take down and kill), the disproportionate presence of prey heads in archaeological sites (Stiner, 2013), and the extensive evidence for meat sharing (Hill et al., 2009; Hill and Hurtado, 2009; Apicella, 2014) all point to the prosocial importance of hunting, rather than to its relevance with subsistence. These results suggest a form of switch selection (Murdoch, 1969) in which a generalist predator (in this case humans) selects the most abundant prey in the habitat it occupies, or when all of the available prey species are patchily distributed over the predator search range (Cornell, 1976). The rank abundance of prey species within the core of human distribution changed along with climatic changes (Fig. 4). Feral horse and wild boar were the species most closely associated to humans up to some 24 ka. At that time, the ice sheets reached their maximum coverage (Clark et al., 2009), and the cold-adapted species (e.g. reindeer) became the most easily available prey (Fig. 4). As the deglaciation started at some 18 ka, the wild boar turned out the most abundant prey again. During the end of the Pleistocene, rapid and intense changes in global temperatures forced large mammal species to long distance dispersal (Raia et al., 2012) far exceeding the latitudinal shifts observed in humans (Pushkina and Raia, 2008). This must have effectively changed the prey spectrum to Paleolithic people a number of times, favoring switches among preferred prey and creating variable threats across different parts of species geographical ranges. This change is also evident at the middle to upper Paleolithic cultural transition (Stewart, 2004). Crucially, we found humans were the species with the greatest climatic similarity with itself (i.e., climatic conservatism) across time (Fig. 5). Interestingly, such strong climatic tolerance is typical of carnivorous mammals as well, and might explain the positive relationship between humans and extant large carnivores (Fig. 2a,c). This is further supported by the evidence that extant carnivores might have overcome end Pleistocene extinction by virtue of such wide climatic tolerance (Di Febbraro et al., 2017). In contrast, extinct large carnivores did show little overlap to humans (Fig. 2a), which suggests they might have gone extinct primarily by climatic effects.

Our results suggest that humans stood their grounds across periods

of changing climates, by modifying natural environments to their needs (Sullivan et al., 2017) and may have opportunistically switched among different prey species as their availability waxed and waned. This has potentially important consequences on prey extinction risk. Because the populations of the most abundant prey are usually controlled by habitat quality, rather than by predation (Hopcraft et al., 2010), by hunting upon the most abundant prey, humans might have unintentionally focused on those enduring the lowest extinction risk. Our findings suggest that *H. sapiens* was not the main factor in Eurasian megafauna extinction, although it is still possible that human exploitation contributed to amplify the vulnerability of some taxa to climate change (Malhi et al., 2016) especially for slow-reproducing prey (Johnson, 2002). It would be interesting to reproduce the same kind of study on New World and Oceania faunas, where the human arrival strikingly coincide with the end Pleistocene large mammals extinction (but see Lima-Ribeiro and Diniz-Filho, 2013; Holen et al., 2017). It would also be interesting to take in consideration species social system (since gregarious species are hard to find, except where the herds roam). Our approach is based on modeled distributions and climatic preferences of species. As with any modelling approach, this has major advantages (scale, ease of interpretation) as well as limitations (resolution, precision). Moreover, an important assumption is that species populations really were more abundant where the habitat was better suited to them. The archaeological record is dense with site-by-site information about prey consumption style and prey choice, derived directly from fossil evidence of human activity on prey carcasses, that could be tested to stress the OFT hypothesis. Despite all of these caveats, this study provides evidence that humans excelled in exploiting their preys during the late Pleistocene, and contrary to the common complaint against Paleolithic hunters, that they could hardly be blamed for the extinction of Eurasian megafauna.

5. Conclusion

Late Pleistocene *Homo sapiens* climatic niche was similar to those of modern, medium-sized herbivores. Although strongly overlapping to humans in terms of geographic range, the extinct megafauna was presumably rare within humans' optimal habitat patches. This suggests that Paleolithic hunters had stronger association to extant rather than extinct herbivorous species. Although climatic coincidence is no direct

proof of human preference in terms of hunting, the results presented here suggest humans had lower opportunity to kill extinct megafauna individuals. Our modelling results concur with evidence coming from the archaeological record, suggesting that medium-sized extant herbivores such as wild boar and deer are more common than extinct megafauna in Late Paleolithic contexts.

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